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Differential effects of canopy trimming and litter deposition on litterfall and nutrient dynamics in a wet subtropical forest

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ABSTRACT

Humid tropical forests have the highest rates of litterfall production globally, which fuels rapid nutrient recycling and high net ecosystem production. Severe storm events significantly alter patterns in litterfall mass and nutrient dynamics through a combination of canopy disturbance and litter deposition. In this study, we used a large-scale long-term manipulation experiment to explore the separate and combined effects of canopy trimming and litter deposition on litterfall rates and litter nutrient concentrations and content. The deposition of fine litter associated with the treatments was equivalent to more than two times the annual fine litterfall mass and nutrient content in control plots. Results showed that canopy trimming was the primary driver of changes in litterfall and associated nutrient cycling. Canopy trimming reduced litterfall mass by 14 Mg ha^{-1} over the 2.5 year post-trim period. Nutrient concentrations increased in some litter fractions following trimming, likely due to a combination of changes in the species and fractional composition of litterfall, and increased nutrient uptake from reduced competition for nutrients. Declines in litterfall mass, however, led to large reductions in litterfall nutrient content with a loss of 143 ± 22 kg N ha^{-1} and 7 ± 0.2 kg P ha^{-1} over the 2.5 year post-trim period. There were no significant effects of litter deposition on litterfall rates or nutrient content, contrary to results from some fertilizer experiments. Our results suggest that large pulsed inputs of nutrients associated with tropical storms are unlikely to increase litterfall production, and that canopy disturbance has large and lasting effects on carbon and nutrient cycling.

1. Introduction

Litterfall is a key conduit for carbon (C) and nutrient recycling in terrestrial ecosystems. Humid tropical forests have the highest rates of litterfall production globally (Raich and Tufekcioglu, 2000; Clark et al., 2001). These ecosystems also have the fastest rates of litter decomposition (Parton et al., 2007; Cusack et al., 2009), leading to rapid turnover of litterfall C and nutrient stocks. Fast rates of litterfall production and decomposition contribute to the high net ecosystem production typical of humid tropical forest ecosystems (Melillo et al., 1993; Malhi et al., 1999).

Canopy disturbances associated with severe storms dramatically alter patterns in litterfall and associated nutrient cycling (Lugo and Scatena, 1996; Scatena and Lugo, 1995). Current estimates from global circulation models suggest that severe tropical storms (i.e., hurricanes, cyclones, and typhoons) are likely to increase in intensity and/or frequency with elevated greenhouse gas emissions and climate change (Zhao and Held, 2012; Villarini and Vecchi, 2013). Declines in litterfall production following severe storms can persist for many years (Scatena et al., 1996, although see Lugo et al., 2011), and thus are likely to decrease nutrient transfers from the canopy to the forest floor, and slow rates of nutrient recycling between plants and soils during the post-storm period. Lower nutrient inputs could ultimately feed back on the tropical forest C cycle over the long term, resulting in lower plant C uptake and higher atmospheric CO_2 concentrations.

The effects of tropical storms on litterfall dynamics result from a combination of canopy reduction and litter deposition. High winds defoliate and break fine and coarse branches in upper and mid-canopy trees, temporarily decreasing litterfall production. Canopy reduction and tree falls create gaps that increase understory light levels (Fernández and Fetcher, 1991) and decrease competition for light and other resources for survivors (Silver et al., 1996), which could in turn increase the growth and litter

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production of surviving vegetation (Fernández and Fetcher, 1991; Lin et al., 2011; Plotkin et al., 2013). Changes in ecosystem structure associated with disturbance can lead to changes in the composition and distribution of litterfall. For example, surviving understory vegetation and new recruitment may differ in the seasonality of litter production (Angulo-Sandoval et al., 2004), the distribution of litterfall fractions (leaves, wood, fruits and flowers, and miscellaneous material), as well as litterfall nutrient concentrations relative to canopy species (Lugo, 1992). Litter deposition associated with severe storms can reduce understory litter production, at least initially, if understory plants are physically damaged or buried by falling debris (Basnet et al., 1992). A large influx of nutrient-rich green plant material can stimulate plant growth and associated litter production through a fertilization effect (Wood et al., 2009), although woody litter can immobilize added nutrients and slow nutrient recycling (Zimmerman et al., 1995).

The different and potentially confounding effects of canopy opening and litter deposition make it difficult to predict the effects of severe storms on C and nutrient cycling during ecosystem reorganization in tropical forests. Here we report on the Canopy Trimming Experiment (CTE), a large-scale long-term experiment in the Luquillo Experimental Forest (LEF), Puerto Rico (Richardson et al., 2010). The CTE included a canopy disturbance treatment, as well as treatments designed to allow us to explore the separate effects of canopy disturbance and litter inputs associated with strong tropical storms. We tested the hypothesis that litter deposition associated with severe storms partially offsets the negative effects of canopy disturbance, leading to greater litterfall production in sites with litter deposition and canopy trimming than with canopy trimming alone. We also tested the hypothesis that patterns in litterfall nutrient inputs would be driven primarily by effects on litterfall mass and not by changes litterfall nutrient concentrations, which were predicted to be relatively insensitive to the manipulations. Finally, we used the CTE to explore seasonal dynamics in litterfall and litterfall nutrients in this relatively aseasonal humid tropical forest.

2. Materials and methods

2.1. Study site and experimental design

The study was conducted in the El Verde research area of the Luquillo Experimental Forest (LEF), Puerto Rico, part of the Long Term Ecological Research program (18°20′N, 65°49′W). The sites were located in the tabonuco forest type at approximately 350 m elevation above sea level. Mean annual air temperature during the study (2003–2009) was 24.2 (±0.1) °C and mean annual precipitation was 3105 (±70) mm (range from 2885 to 3405 mm y^{-1}). January through April are drier months, with average monthly rainfall 275 mm mon^{-1} (Heartsill-Scalley et al., 2007).

Soils in the research area are dominantly Oxisols in the Zarzal complex, derived from volcanoclastic sediments. These soils are clay rich, deeply weathered, and depleted in most primary minerals (Soil Survey Staff, 2002). The tabonuco forest type is characterized by approximately 190 tree species (Scatena, 1989). Vegetation at the site was dominated by *Dacryodes excelsa* (Vahl), *Prestoea montana* (Vahl), *Manilkara bidentata* ((A.DC.)A.Chev.) and *Sloanea berteroana* (Choisy) (Shiels et al., 2010). There are two main peaks of leaffall observed in this forest, which coincide with the periods of major solar radiation at this latitude (Zalamea and González, 2008).

We used a complete randomized block design with three replicate blocks each containing four 30 × 30 m treatment plots separated by approximately 20 m buffers. Within each plot, a 20 × 20 m sampling area was defined and furthered divided into 16 subplots to minimize the effects of destructive sampling on long-term measurements. Treatments consisted of: (1) canopy trimming and litter deposition (trim + debris), (2) canopy trimming with the litter removed (trim + no debris), (3) intact canopy with litter added from the removal treatment (no trim + debris) and (4) no manipulation (no trim + no debris). Pre-treatment litterfall measurements began in November 2002. The manipulations spanned from late October 2004 to June 2005. Each treatment was completed within a given plot and block before the subsequent block was treated. Details of the treatments, plots, and timing are given in Shiels et al. (2010) and Richardson et al. (2010). Trimmed material was weighed using tarps and spring balances. Canopy trimming generated approximately 72 ± 2 Mg ha^{-1} of necromass. The necromass was not immediately distributed on the plots resulting in some loss of mass (Richardson et al., 2010; Shiels et al., 2010), and associated nutrient changes (Shiels and González, 2014). To determine the nutrient deposition from fine litter generated from trimming, we multiplied the dry mass (1.6 Mg $plot^{-1}$) of leaves (which were pooled with fine twigs) by the mean annual nutrient concentrations in leaf litterfall in the same forest, using data generated from the unmanipulated plots (no trim + no debris) (Table 1). We used litterfall concentrations as opposed to values for fresh plant fractions because of potential nutrient loss prior to placement on the experimental plots (Shiels and González, 2014). This resulted in an estimated minimum nutrient deposition rate of 164 kg N ha^{-1}, 5 kg P ha^{-1}, 34 kg K ha^{-1}, 157 kg Ca ha^{-1}, and 40 kg Mg ha^{-1}. These are minimum values because additional nutrients were added in other litter fractions (fine and coarse wood, fruits and flowers, and miscellaneous material) that were not quantified during the trimming events but were deposited on the plots.

Litterfall was collected every 14 days from 10 baskets (dimensions 43 × 43 cm) distributed in a stratified random fashion (to ensure plot coverage) inside each 20 × 20 m core area of each treatment plot. Baskets were leveled and fastened to poles at 1 m height. Baskets were removed during the trimming of respective treatment plots in order to prevent the baskets from getting broken by dropped branches, and replaced as soon as the canopy trimming was completed.

We separately report the pretreatment (November 2002–October 2004) and post-treatment (July 2005–December 2007) data, recognizing that this excludes a small amount of data during the establishment of the experiment. Litterfall mass associated with the trimming events was estimated by weighing the litter generated during the canopy manipulation using tarps and spring balances. Following each litter collection, litter was dried at 40 °C for at least one week, and kept in a heated room until samples could be sorted into the following categories: leaves, wood, fruits and flowers (including seeds), miscellaneous (unidentifiable material >2 mm). We re-dried subsamples of litterfall at 65 °C and weighed them to establish a conversion to oven dry weight. Litterfall was pooled by fraction within each plot quarterly for chemical analyses. In this paper we report quarterly mass to compare with nutrient concentrations and nutrient content.

2.2. Laboratory procedures

Litterfall samples were ground to pass through an 18 mesh sieve. Total C and N were determined using the macro dry combustion method on a LECO TruSpec CN Analyzer or LECO CNS-2000 Analyzer. The LECO CNS-2000 Analyzer was used to determine total C and N of litterfall in 2002–2004. The remaining total C and N analyses were determined utilizing the LECO TruSpec CN Analyzer. Blanks and reference materials were analyzed with each run at a rate of 1 per 10–20 samples to insure that the samples were directly comparable.

Table 1
Annual mass and elemental concentrations of litterfall in control plots in the Luquillo Experimental Forest, P.R. Values are means and standard errors over 5 years. Different letters indicate statistically significant differences among litter fractions ($P < 0.05$).

	Leaves	Fruits and flowers	Wood	Miscellaneous
Mass (g/m^2)	555 ± 20a	142 ± 25b	150 ± 14b	36 ± 3c
Carbon (%)	53 ± 0.22a	55 ± 0.31b	54 ± 0.20c	54 ± 0.24d
Nitrogen (%)	0.94 ± 0.02a	1.28 ± 0.04b	0.81 ± 0.02c	1.82 ± 0.04d
Phosphorus (mg/g)	0.27 ± 0.01a	1.02 ± 0.03b	0.29 ± 0.02a	1.00 ± 0.04b
Calcium (mg/g)	9.00 ± 0.30a	4.61 ± 0.25b	10.08 ± 0.35c	9.30 ± 0.43ac
Magnesium (mg/g)	2.29 ± 0.09a	1.69 ± 0.07b	1.90 ± 0.06c	2.25 ± 0.06a
Potassium (mg/g)	1.94 ± 0.10a	4.70 ± 0.20b	1.77 ± 0.08a	2.73 ± 0.10c
Iron (mg/g)	0.57 ± 0.40a	0.23 ± 0.05a	0.14 ± 0.01a	0.67 ± 0.04a
Manganese (mg/g)	0.61 ± 0.03a	0.24 ± 0.02b	0.44 ± 0.02c	0.52 ± 0.02d
Aluminum (mg/g)	0.47 ± 0.14a	0.24 ± 0.02a	0.29 ± 0.05a	0.97 ± 0.07b
N:P ratio	36 ± 1.3a	13 ± 0.5b	30 ± 1.0c	20 ± 1.4d
C:N ratio	57 ± 1.1a	46 ± 1.5b	69 ± 1.6c	31 ± 1.1d

The ground litterfall samples were digested using a modification of the method recommended by Chao-Yong and Schulte (1985). This wet oxidation uses concentrated HNO_3, 30% H_2O_2 and concentrated HCl and was achieved using a digestion block with automatic temperature control. The digests from 2002 to 2005 were analyzed on a Spectro Ciros ICP Emission Spectrometer, and those from 2006 to 2008 were analyzed in a Spectro Spectro-Blue ICP Emisson Spectrometer, all for Ca, K, P, Mg, Fe, Al, and Mn. The results are reported as mg g^{-1} on a dry basis at 105 °C. Blanks and National Institute of Standards certified reference material was analyzed with every run for quality assurance and quality control. The moisture factor correction at 105 °C was determined by the LECO Thermogravimetric Analyzer, model TGA 701 and applied to all reported values. All laboratory procedures were conducted at the International Institute of Tropical Forestry in Puerto Rico. Carbon:N and N:P ratios were calculated using mass weighted values.

2.3. Statistical analyses

We tested treatment effects on litterfall and litterfall nutrients over time using additive mixed models fit in the mgcv package in R (Wood, 2006). Additive models fit smoothed spline functions to data by determining a statistically optimal degree of curvature during model fitting. This method allows parsimonious estimation of non-linear temporal trends that may vary among treatments. We included random effects in these models for blocks and plots to account for spatial correlation and repeated sampling; inclusion of autoregressive error terms did not significantly improve model fit. Model fitting was initially conducted using the raw data, and response variables were log-transformed as necessary to satisfy model assumptions (noted below).

Model selection was conducted for each response variable as follows: the initial model included a fixed effect for canopy trimming treatment and a separate smooth function over time for the trimmed and unmanipulated treatments. Analogous separate models were used to assess effects of litter addition and interactions between trimming and litter addition. We found no evidence for interactions between the canopy trimming and litter deposition treatments. We therefore focused our analysis on main treatment effects: *trimming*, which included the trim + debris and trim + no debris treatments, and *litter deposition*, which included the no trim + debris and trim + debris treatments. Quarter of year was also included as a fixed effect to account for intra-annual variation. We assessed the significance of overall differences in treatment means and quarters using F tests. Differences in temporal trends between treatments were assessed by comparing a model that contained a separate smooth function for each treatment over time with a reduced model that contained a single smooth function for both treatments (i.e., trimming and litter deposition). These models were then compared using likelihood ratio tests. Thus, we were able to assess treatment differences using two separate metrics: overall differences in treatment means regardless of timescale, and differences in temporal trends between treatments as assessed by smooth functions. Using both of these metrics was necessary because in some cases treatment responses were relatively brief in comparison to the overall period of measurement. Models were initially fit to post-treatment data (including data after the first quarter of 2005 for blocks A and C and last quarter of 2004 for block B), and when treatment effects were significant, models were also fit to pre-treatment data to test for differences among plots prior to treatment application. Pre-treatment differences were not significant for any case where plots differed after treatments were applied. We report the means and standard errors of the six plots per trimming or litter deposition treatment, and three unmanipulated plots per time period.

3. Results

3.1. Background patterns in litterfall mass and nutrients

Annual litterfall mass averaged 883 ± 71 g m^{-2} in the control plots over the 5 year study with little inter-annual variability. Leaf litter accounted for 63 ± 3% of total litterfall (Table 1). Fruits and flowers and wood contributed 16 ± 5% and 17 ± 1%, respectively, while miscellaneous material amounted to only 4 ± 0.4%. Fruits and flowers and miscellaneous material had the highest concentrations of N and P, while wood and leaves had the highest concentrations of Ca and Mg. Miscellaneous material had very high concentrations of Al (0.97 ± 0.07 mg g^{-1}). In general, the average nutrient mass of litterfall followed similar patterns as litterfall mass with a few exceptions: fruits and flowers contained disproportionally high amounts of the average annual litterfall P (37 ± 8%) and K (31 ± 8), while leaf litter had only 42 ± 7% and 52 ± 6% of the total litterfall P and K, respectively (Table 1).

Litterfall mass and nutrient concentrations varied over quarterly time scales (Fig. 1a–d). Leaf litterfall mass was lowest in the first three months (December–February) and peaked in the second quarter ($p < 0.001$). Fruit and flower production peaked in the third quarter ($p = 0.001$). Temporal patterns in litterfall nutrient concentrations often differed significantly by fraction and nutrient. Leaf litterfall N was lowest in the second quarter ($p < 0.001$, quarter effect) and C:N ratios were highest ($p < 0.0001$, quarter effect) in the second and third quarters. Leaf litterfall P and Fe were also lower in the second quarter of the year ($p < 0.001$ and $p < 0.0001$

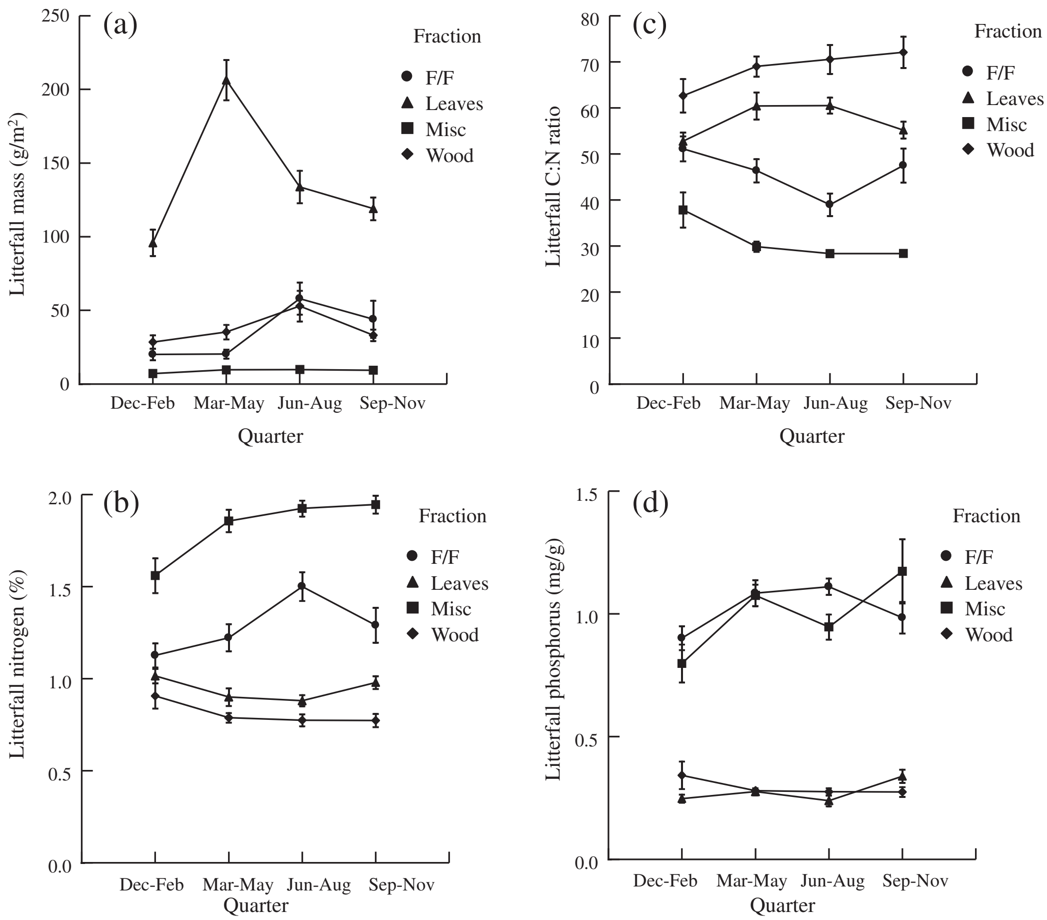

Fig. 1. Quarterly patterns in (total) litterfall mass and chemical properties in the control (no trim + no debris) plots in the Luquillo Experimental Forest, Puerto Rico (2003–2007); (a) litterfall mass, (b) nitrogen concentration, (c) C:N ratio and (d) phosphorus concentration. Values are means and standard errors. F/F refers to fruits and flowers, and misc refers to the miscellaneous fraction.

for quarter effects, respectively). The Al concentrations of fruits and flowers and the K concentrations in the miscellaneous material were lowest in the first quarter, while K in fruits and flowers was lowest in the third and fourth quarters and greatest in the second quarter ($p < 0.0001$ for quarter effects, data not shown).

3.2. Effects of canopy trimming

Canopy trimming led to a significant increase in leaf litterfall N, P, and Fe concentrations (Fig. 2a–d). Leaf litter N increased by up to 23% relative of the untrimmed treatments during the 2.5 y post treatment period, with an average increase of 15 ± 3% in the canopy trimming treatments over the same period ($p < 0.05$). Higher leaf litterfall N concentrations led to significantly lower C:N ratios following trimming ($p < 0.03$) and different temporal trends between trimmed and untrimmed plots ($p < 0.01$). Leaf litterfall N and C:N ratios both had returned to the level of the unmanipulated plots by the end of the experiment. Leaf litterfall P concentrations increased by up to 11% in the trimmed treatments (0.38 ± 0.01 mg P g^{-1}) relative to the untrimmed plots (0.30 ± 0.01 mg P g^{-1}), with an average increase of 5 ± 3% over the 2.5 y following the treatments; trends in leaf litterfall P differed significantly between the trimmed and the untrimmed treatments over this interval ($p = 0.02$), although overall means did not significantly differ when the entire post-treatment period was considered. Leaf litterfall Fe concentrations increased slightly, but significantly (log transformation, $p < 0.0001$) following canopy trimming and had not returned to pre-disturbance levels by the end of the experiment (Fig. 2d).

Canopy trimming significantly increased the concentrations of K in woody litter ($p < 0.01$), and decreased wood Ca concentrations ($p < 0.01$) (Fig. 3a–c). Wood Ca appeared to recover, but K concentrations were still significantly elevated relative to the untrimmed plots at the end of the experiment. There were no significant effects of canopy trimming on nutrient concentrations of fruits and flowers. However, the Al concentrations of fruits and flowers increased significantly following trimming (Fig. 4a, log transformation; $p < 0.05$). Similarly, the Al concentrations of the miscellaneous material were higher in the trimmed plots following the treatment (log transformation; $p < 0.05$), and remained elevated until the end of the experiment 2.5 y later (Fig. 4b). Concentrations of Fe were significantly higher in the miscellaneous material following trimming (log transformation; Fig. 4c; $p < 0.0001$). The only significant effects of litter deposition on elemental concentrations were higher K in the miscellaneous material in the deposition plots (Fig. 4d, $p < 0.05$), and a significant temporal trend toward increased leaf K concentrations at the end of the experiment ($p < 0.05$; overall means were not significantly different).

Over the first 2.5 y post-treatment, total litterfall mass averaged 8 ± 1 Mg ha^{-1} in the plots with trimmed canopies, and was significantly lower than the untrimmed plots (23 ± 1 Mg ha^{-1}) (Table 2, $p < 0.0001$). Litterfall production had not recovered by the end of the experiment (Fig. 5). This resulted

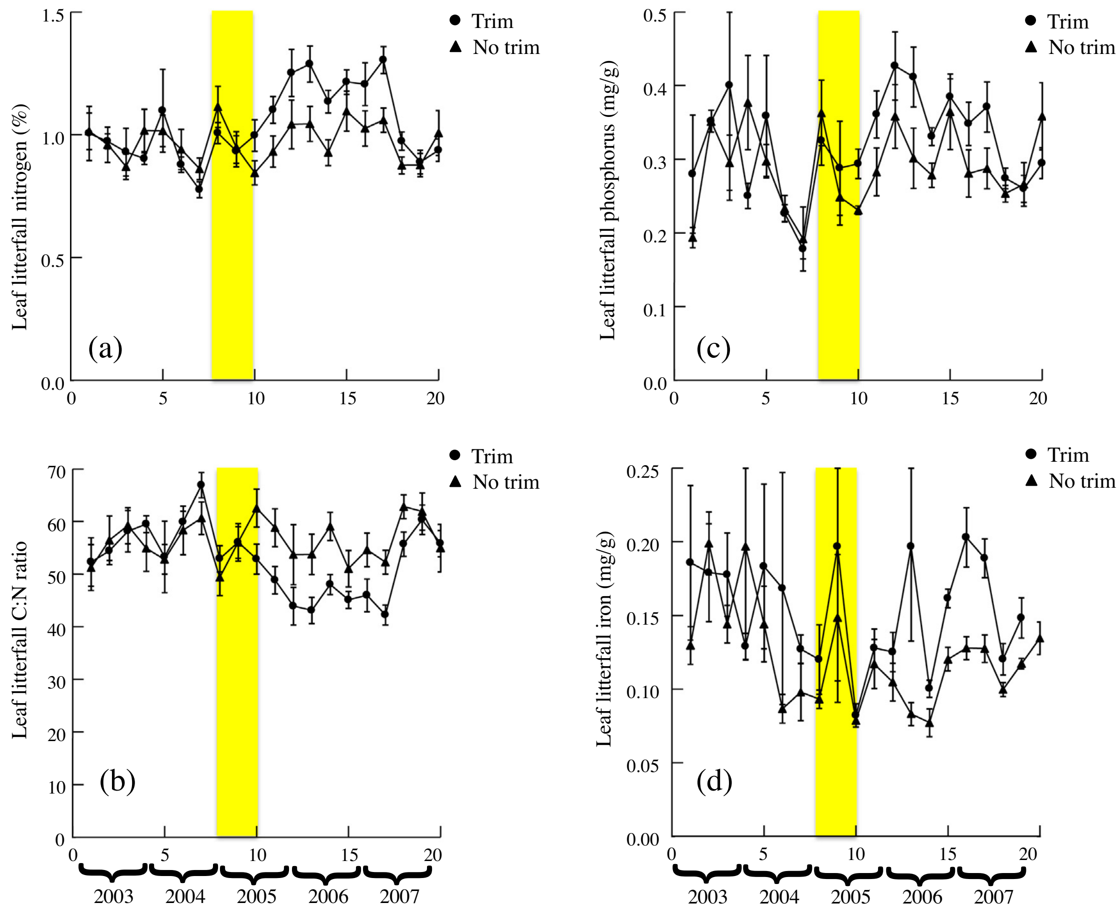

Fig. 2. Effects of canopy trimming (trim + debris and trim + no debris) relative to untrimmed treatments (no trim + debris and no trim + no debris) on leaf litterfall chemical properties from in the Luquillo Experimental Forest, Puerto Rico. Trim treatments are represented by circles and no trim treatments are represented by triangles. Yellow bars indicate the period of treatment establishment; (a) nitrogen, (b) C:N ratio, (c) phosphorus and (d) iron; note that two outliers of 23 and 2.6 mg Fe g^{-1} were removed. Values are means and standard errors. *X*-axis values refer to the 4 month period sampled. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

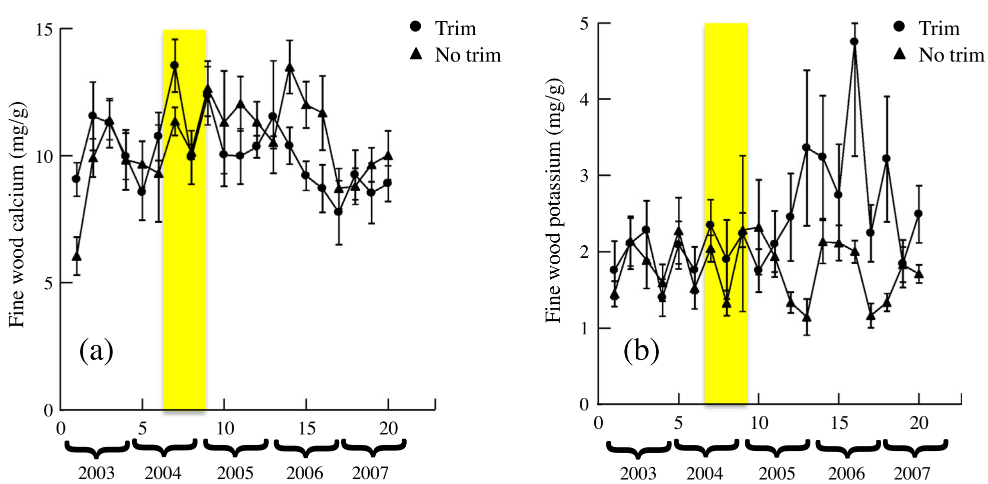

Fig. 3. Effects of canopy trimming on fine wood litterfall chemical properties from in the Luquillo Experimental Forest, Puerto Rico. See Fig. 2 for definitions of the treatments. Yellow bars indicate the period of treatment establishment; (a) calcium and (b) potassium. Values are means and standard errors. *X*-axis values refer to the 4 month period sampled. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in significant declines in litterfall P inputs from 11 ± 0.8 kg P ha^{-1} to 4 ± 0.6 kg P ha^{-1} and litterfall N inputs from 236 ± 21 kg N ha^{-1} to 93 ± 16 kg N ha^{-1} (Table 2). Of the base cations, Ca inputs showed the greatest decline in trimmed plots, followed by K and Mg. Canopy trimming significantly decreased the proportions of leaves ($p < 0.01$) and fruits and flowers ($p < 0.05$) in litterfall for the 2.5 y following the treatments relative to untrimmed plots. There was no significant effect of the litter debris addition

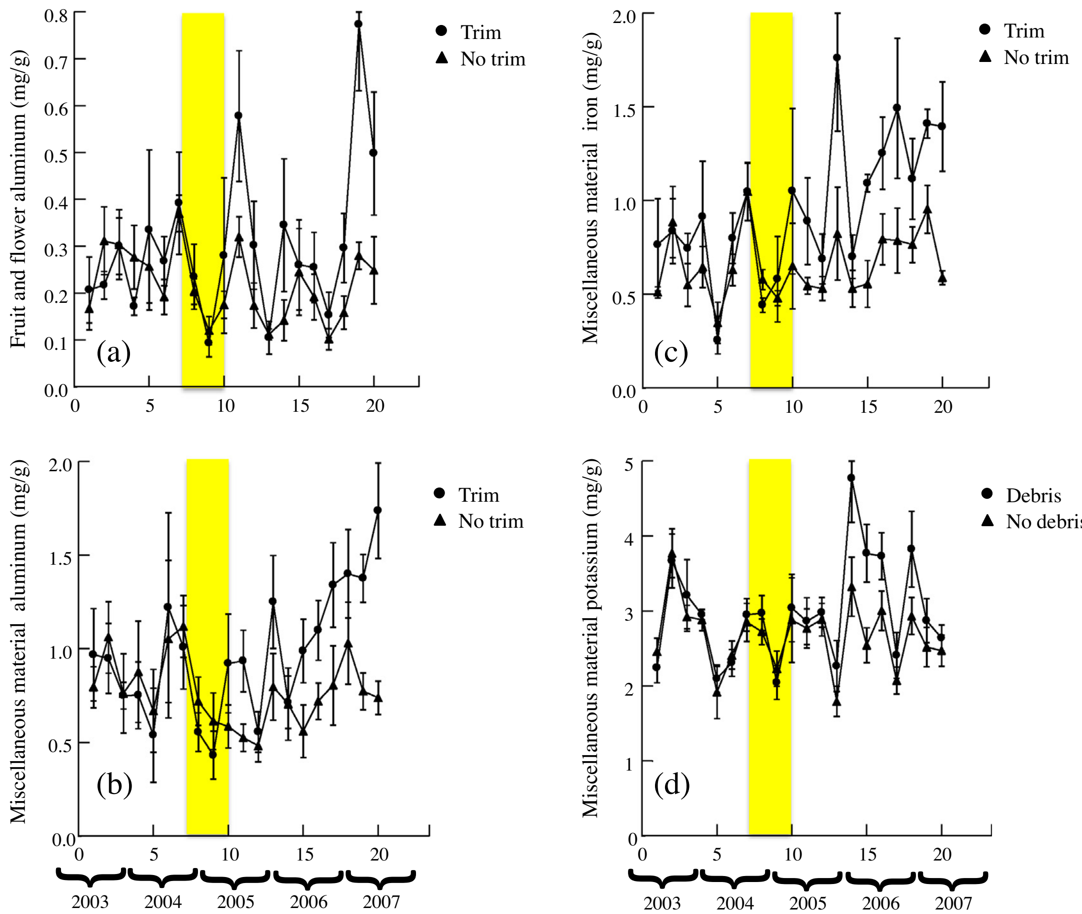

Fig. 4. Effects of canopy trimming or debris deposition on fruit and flower and miscellaneous material litterfall chemical properties from in the Luquillo Experimental Forest, Puerto Rico. See Fig. 2 for definitions of the trimming treatments. Deposition includes trim + debris and no trim + debris treatments. No deposition includes no trim + no debris and trim + no debris treatments. Yellow bars indicate the period of treatment establishment; (a) fruit and flower aluminum, (b) miscellaneous aluminum, (c) miscellaneous iron and (d) miscellaneous potassium. Values are means and standard errors. *X*-axis values refer to the 4 month period sampled. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
The difference in litterfall mass and elemental inputs from canopy trimming relative to intact canopies during the first 2.5 y following the manipulation in the Luquillo Experimental Forest, P. R. values are means and standard errors and are in kg/ha except for mass and C which are in Mg/ha.

Mass	−14 ± 1
C	−8 ± 0.5
N	−143 ± 22
P	−7 ± 0.2
Ca	−126 ± 6
Mg	−28 ± 3
K	−37 ± 2
Fe	−1.7 ± 0
Mn	−8 ± 1.3
Al	−1.8 ± 0.2

treatment on nutrient transfers in litterfall at this temporal scale of resolution.

4. Discussion

4.1. Litterfall dynamics in intact forest

Background litterfall productivity (i.e., not influenced by treatment effects) over the 5 y study was similar to other humid tropical forests (Clark et al., 2001; Chave et al., 2010) and very similar to values for a nearby tabonuco forest site (869 ± 66 g m^{-2} y^{-1}) in the LEF (Scatena et al., 1996). The N and P concentrations, and thus N and P return in litterfall, were at the low end of sites on moderately fertile soils reviewed in Sayer and Tanner (2010). In this study, fruits and flowers contributed approximately one third of the annual litterfall P and K fluxes while representing only 16% of total litterfall mass. This high nutrient allocation to reproduction may be part of a strategy to attract pollinators and/or dispersers, or result from the relatively low herbivore pressure in the LEF (Bazzaz et al., 1987). The miscellaneous fraction of litterfall had high Al concentrations. Aluminum is not a nutrient element and generally considered toxic to most higher organisms (Delhaize and Ryan, 1995). Miscellaneous material was likely a combination of leaf fragments and fruits and flowers that tend to be fragile and easily friable. Some tropical plants are known to be Al accumulators, and may take up Al to facilitate root P acquisition (Jansen et al., 2000) or deter herbivores (Pilon-Smits et al., 2009).

Quarterly litterfall fluxes varied over an annual cycle, driven primarily by patterns in leaf litter production. Temporal patterns in leaffall are likely due to seasonality in light availability (Scatena et al., 1996; Zimmerman et al., 2007; Zalamea and González, 2008). Zalamea and González (2008) found that species differed in their leaffall seasonality. We found that leaf litterfall peaked in the second and third quarters of the year, corresponding to lower N and P concentrations and higher C:N ratios. Temporal differences in litterfall quantity and quality could feed back on patterns in decomposition and nutrient fluxes over the year.

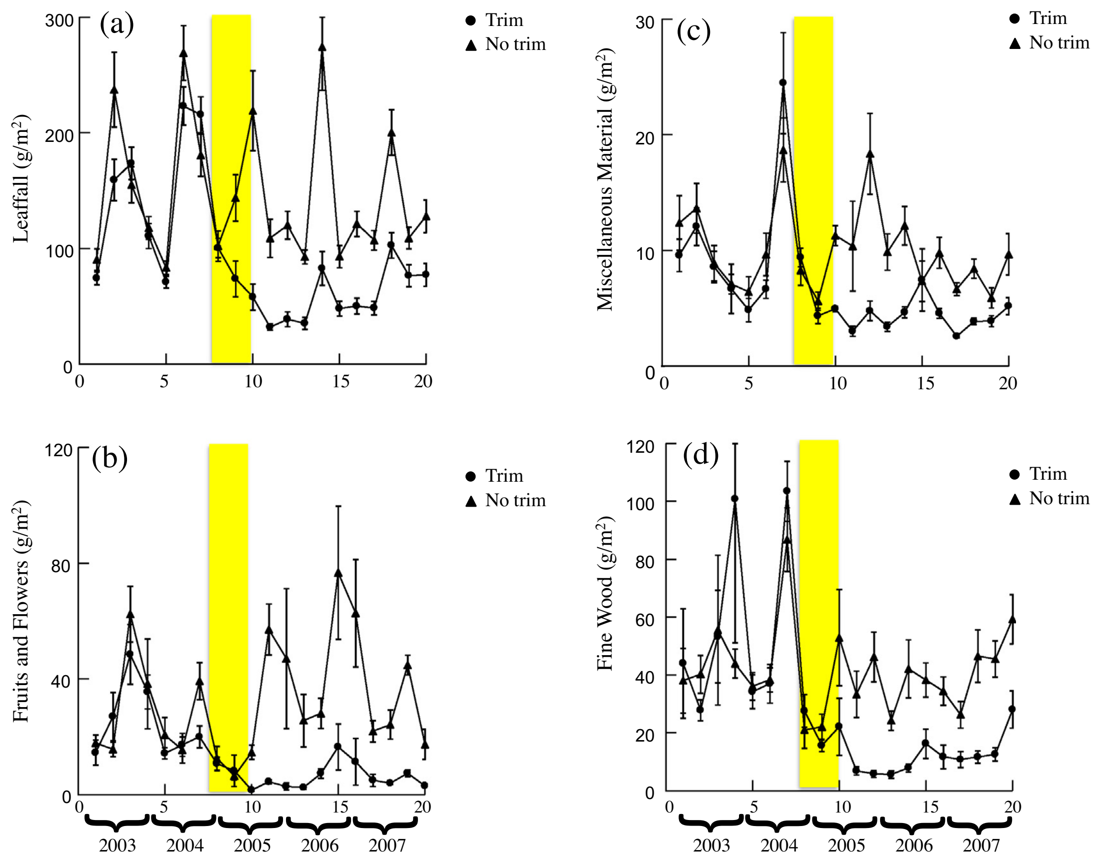

Fig. 5. Effects of canopy trimming on litterfall mass from in the Luquillo Experimental Forest, Puerto Rico. See Fig. 2 for definitions of the treatments. Trim treatments are represented by circles and no trim treatments are represented by triangles. Yellow bars indicate the period of treatment establishment; (a) leaf litterfall, (b) fruits and flowers, (c) miscellaneous material and (d) fine wood. Values are means and standard errors. *X*-axis values refer to the 4 month period sampled. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.2. Effects of canopy trimming and litter deposition

Canopy trimming had a large and lasting effect on litterfall mass and nutrient dynamics. Litterfall mass in the trimmed plots had not recovered to pre-treatment levels 2.5 y after the manipulation. Previous research has also shown that litterfall rates can be slow (>5 y) to recover from canopy disturbance in the mature forest of the LEF (Scatena et al., 1996), although faster recovery rates have been measured in secondary forests (Lugo et al., 2011). Litterfall rates were the dominant factor controlling nutrient fluxes in litterfall following trimming. Phosphorus return in litterfall was only 35 ± 3% and litterfall N was only 40 ± 6% of the intact sites for the 2.5 y post treatment period. Fruit and flower production decreased by almost half following canopy trimming. This coupled with the relatively high concentrations of P and N in this litterfall fraction contributed to slower P and N cycling between plants and soils in this ecosystem.

Leaf litterfall N and P concentrations increased in the trimmed plots relative to those with an intact canopy. Other studies have reported increased litterfall nutrient concentrations following storms (Waterloo, 1994; Scatena et al., 1996). This has been attributed to changes in species composition, a relative increase in the contribution of herbaceous and understory species in litterfall, and the delayed inputs of "hanging litter", defined as green plant material forcibly senesced during the storm but not immediately deposited on the forest floor (Lodge et al., 1991; Scatena et al., 1996). The design of the current experiment eliminates suspended green litter as a contributor to higher post disturbance nutrient concentrations. Thus, changes in the composition of litterfall are likely responsible for the patterns observed, as well as potential physiological changes in survivors, such as more rapid leaf turnover or higher nutrient uptake due to lower competition for nutrients. Leaf litterfall Fe concentrations also increased following canopy trimming. Decreased transpiration associated with lower leaf area likely contributed to higher soil moisture levels recorded in the trimmed plots (Richardson et al., 2010). Higher soil water content can lead to low redox events (Silver et al., 1999; Hall et al., 2013) and associated Fe reduction (Chacón et al., 2006). Reduced Fe is more mobile than oxidized forms, and thus more easily assimilated by plant roots. Iron reduction has also been associated with P mobilization in these soils (Chacón et al., 2006), and may help explain higher leaf litter P concentrations in the trimmed plots.

Canopy trimming significantly increased K concentrations in wood and led to a short-term decrease in wood Ca. Few studies have explored the effects of disturbance on the nutrient concentrations of litterfall wood fractions. We expect that the increase in wood K concentrations was due to a combination of changing species composition and an increase in K availability as a result of decreased competition for nutrients. Aluminum concentrations increased in the fruits and flowers and miscellaneous material following canopy trimming. As mentioned above, the miscellaneous material was probably dominated by fragments of leaves and fruits and flowers, and thus reflects the elemental content of that material. If soil pH decreased as a result of the disturbance due to increased inputs of dissolved organic acids, this could increase Al mobilization and uptake (Pilon-Smits et al., 2009). Silver et al. (1996) reported an increase in soil acidity and exchangeable Al concentrations in soils following tree harvesting in the LEF. Large disturbances often stimulate nitrification and NO_3^- leaching, which can lower pH and mobilize Al in these soils (Silver and Vogt, 1993; Silver et al., 1996; McDowell and Liptzin, 2014).

Contrary to our hypothesis, there was almost no effect of litter deposition on litterfall mass or nutrient content. Results of litter manipulation studies and fertilization experiments in tropical forests have produced conflicting results. For example, Sayer et al. (2012) found that doubling monthly litter inputs beneath an intact canopy increased litterfall N in a lowland tropical forest in Panama. However, they found no effect of increased litter deposition on other litterfall nutrients, and found little effect on litterfall production. In a humid lowland tropical forest in Costa Rica a one-time litter addition (4-fold increase over the standing crop) increased litterfall production; the effect varied seasonally but persisted for at least 1.5 years (Wood et al., 2009). In that study, the authors reported no significant effects of litter additions on litterfall nutrient concentrations.

Fertilization experiments in tropical forests also do not show consistent effects on annual litterfall and litterfall nutrient concentrations, reporting both stimulation (e.g., Tanner et al., 1992; Harrington et al., 2001; Yang et al., 2007; Kaspari et al., 2008; Adamek et al., 2009; Homeier et al., 2012; Lu et al., 2012; Zimmerman et al., 1995), or no effect (e.g., Cusack et al., 2011; Sayer et al., 2012; Alvarez-Clare et al., 2013). The varied results suggest that ecosystem responses are highly dependent upon soil, climate, plant community characteristics, and/or experimental conditions (i.e., addition rates, timing, and nutrient composition(s)). A complete fertilizer addition significantly increased litterfall production for approximately 20 months following a hurricane in the LEF (Zimmerman et al., 1995); however, fertilizer was added at twice the rate of N and 20 times the P as was deposited in debris in this study and was added in a more labile form. Furthermore, fertilizer was added every three months for three years, as opposed to the single pulse addition following the canopy trimming treatments. The addition of more nutrients, particularly P that may be limiting to tropical forest plant growth (Cleveland et al., 2011), and the more continual low-level additions likely facilitated greater plant uptake and utilization. Sayer et al. (2012) compared a fertilization experiment with litter addition under an intact canopy and found that litterfall and nutrient content appeared to be more sensitive to nutrients added in litterfall than nutrients applied as inorganic fertilizer, potentially due to direct nutrient cycling from decomposing litter (Stark and Jordan, 1978) or more favorable nutrient stoichiometry in litter (Kaspari et al., 2008). Nutrient inputs from the leaf deposition treatments here were approximately equivalent to 2.5 times the annual fine litterfall values in this forest. Thus, the lack of a response in litterfall or litterfall nutrient concentrations in the deposition treatments suggest that litter pulses associated with storms are not likely to increase the production of litterfall, or that litterfall was not strongly limited by nutrients at this scale of resolution.

5. Conclusions

Our results showed that the effects of canopy trimming, and not debris deposition, were the dominant drivers of patterns in litterfall and litterfall nutrient concentrations following disturbance. Canopy trimming led to a decrease in litterfall mass of 14 Mg ha^{-1} summed over 2.5 y; rates had not recovered by the end of the experiment. Although canopy trimming led to an increase in some nutrient concentrations, the large decrease in litterfall mass resulted in significant declines in nutrient inputs to the forest floor over time. There was no effect of debris deposition on litterfall rates suggesting that litter production in this forest was not sensitive the large pulse of nutrients added. Our results highlight the important roles of ecosystem and community dynamics in controlling nutrient recycling between plants and soils. Future research should explore the effects of canopy trimming and litter deposition on soil C and nutrient dynamics, as these will help determine the long-term implications of changes in the frequency and magnitude of tropical storms with climate change.

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